Host Plant and Habitat Effects on Behavior, Survival, and Growth of Early Instar *Dichomeris leuconotella* (Lepidoptera: Gelechiidae), Leaf-folders on Goldenrods

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Abstract. The relative success with which caterpillars use different host plant species is determined by a variety of factors including host plant food quality, phenology, morphology, and associated predator loads. These factors vary among habitats, and such variation might account for the restriction of some caterpillar species to particular habitats, when their host plant species are more widespread. I studied the effects of host plant and habitat factors on survival and growth of *Dichomeris leuconotella* caterpillars, which occur only in open habitats although their host plants, *Solidago* and *Aster* spp., are widely distributed in forest and field. This paper focuses on early instars.

In larval transplant experiments, differences between host plant species in both food quality and leaf morphology greatly affected caterpillar performance, but differences between habitats on the same host had unexpectedly minor impact and actually slightly favored performance in forests. On an abundant forest goldenrod, *S. caesia,* first and second instars had poor growth rates and high mortality, even when protected from predators; but on *S. rugosa,* which grows in both habitats, unprotected caterpillars grew and survived slightly better in forest than in field, and protected caterpillars performed comparably in the two habitats. Early instars began feeding as quickly on *S. caesia* from forest as on *S. rugosa* from either field or forest; and once started, they could fold *S. caesia* leaves faster than those of *S. rugosa* from either habitat (especially field). However, they took much longer to find suitable sites to spin refuges on the smooth, obscurely veined leaves of *S. caesia*; and they abandoned leaf refuges readily on *S. caesia.* Observations of other leaf-folding caterpillar species suggest that *S. caesia* is best suited as a host for spring-hatching species whose youngest larvae can find "ready-made" refuge in the leafy terminal bud available at that time.

Key Words: Caterpillar, *Dichomeris,* Gelechiidae, habitat, host plant, leaf folder, leaf roller, leaf tier, *Solidago*

Introduction

Several authors have pointed out that the quality of a host plant for an insect herbivore must be a function of many variables; although nutrient content and secondary chemistry are the most often studied, plant morphology, phenology, density, distribution, and associated predators may also have important effects (reviews in Rausher 1983, Bernays and Graham 1988,

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Thompson 1988, Zwolfer and Romstock-Volkl 1991; specific examples in Wiklund and Ahrberg 1978, Mopper *et al.* 1984, Gall 1990, Nylin and Janz 1993). All of these factors vary among habitats, and there are many cases of herbivorous insects attacking a host plant species in one habitat but not another (Shapiro and Carde 1970, Tahvanainan 1975, Rausher 1979 and references therein, Courtney 1984, MacGarvin *et al.* 1986). Understanding the complex interactions of host plant attributes and habitat effects in determining insect distributions requires a combination of approaches: studies designed to test the insect's response to particular host plant attributes, including attributes that vary among habitats, and also experiments that evaluate the insect's performance under a range of natural conditions where all variables (including any that are unknown to the experimenter) are combined. Such studies are rare.

Caterpillars of *Dichomeris leuconotella* (Busck) (Gelechiidae) are habitat-restricted, occurring only in fields and other large open areas such as roadsides or streambanks. Some of their hosts, field goldenrods (*Solidago* spp.) and asters (*Aster* spp.), also occur sparsely in forests; and additional species, especially the abundant goldenrod *S. caesia* L., grow strictly in forests. The caterpillars, which are leaf-folders, will feed and fold leaves on these strictly forest species in the laboratory, although they do not occur on them naturally (Loeffler 1994). Their small size (1 mm at hatching) and prolonged larval development (>4 months on the plants) could make them especially sensitive to leaf characteristics such as thickness, shape, and hairiness, because these characteristics can determine how quickly a caterpillar constructs a leaf fold, the final size and shape of the fold, the caterpillar's manner of feeding, and other factors affecting the fold's value as a refuge from natural enemies and the elements (e.g., Neto 1991). These leaf features vary widely among species of goldenrods and asters, and also among habitats: for example, goldenrods and asters growing in shaded areas have thinner and generally less hairy leaves than those growing in sun.

This paper reports on the relative effects of habitat and host plant factors on the survival and growth of early instar *D. leuconotella* in late summer. Observations on older instars, which mature in the following spring, will be presented in a separate paper. I used larval transfer experiments to evaluate caterpillar performance between habitats and host plants under natural conditions, and I combined caging experiments and behavioral observations to assess roles of specific factors such as predators, host plant chemistry, and leaf characteristics on early instar caterpillar performance. Staged encounters have verified that once a leaf fold or crinkle is spun, it provides effective protection from arthropod predators and dislodgment regardless of whether the leaf is thick and hairy (field-grown *S. rugosa* Aiton leaves) or thin and smooth (*S. caesia* leaves) (Loeffler 1996a and unpublished data). In the present study, therefore, one particular concern was determining the effects of host plant species and habitat on the relative amount of time spent without a refuge (i.e., feeding outside or changing refuges).

The Caterpillars

In central New York, *D. leuconotella* moths oviposit in July on the undersides of goldenrod and aster leaves (Loeffler 1994). The larvae hatch in late July or early August and spin small webs on the leaf undersides. As they grow, they add more silk to the web, gradually pinching and eventually folding the leaves. By early October, when the plants senesce, the caterpillars are third and fourth instars, typically 3-4 mm in length. They overwinter in leaf litter and climb up onto new plants in late April to mid May. They then grow rapidly, change leaf folds with increasing frequency, and reach 15-17 mm in length before pupating in leaf folds in mid- to late June (Loeffler 1994).

Study Sites

The two study sites, Brookshead Reserve and Gowan Farm, are located near the southern edge of the Cayuga Lake Basin in central New York. Each site consists of a large field (>2 ha) and extensive adjacent forest. Goldenrods and asters dominate the fields and grow as scattered clumps and single plants in the forests. The relative abundance and distribution of various species of goldenrods and asters is typical for fields and forests in central New York.

The Gowan Farm field (3.3 km southeast of Brooktondale, NY; elevation 400 m) was originally hayfield and the goldenrods and asters there tend to grow in clones interspersed with grass. *Solidago rugosa* and *S. altissima* L. are common; *Aster lateriflorus* (L.) Britton, *Euthamia graminifolia* (L.) Nuttall, *S. juncea* Aiton, and *S. gigantea* Aiton are present but rare. *Fraxinus americana* L. saplings grow thickly in some spots, mixed with *Rubus* sp. In the forest, under a canopy of mixed northern hardwoods, grow numerous scattered *S. rugosa* and *S. caesia;* some areas also support *Aster divaricatus* L., *A. lateriflorus, S. bicolor* L., and occasional patches or single ramets of other species. All of these species intermingle to some extent, but *S. rugosa* tends to predominate along old fencelines or in younger stands of *Acer saccharum* Marshall, *Betula lenta* L., or *Carya* spp. *Solidago caesia* is most frequent in a mature woods of *Fagus grandifolia* Ehrhart and *Acer saccharum,* whose pit-and-mound topography indicates a history as woodlot rather than agricultural field. Tree seedlings, grasses, sedges, *Caulophyllum thalictroides* (L.) Michaux, *Podophyllum peltatum* L., *Rubus* sp., and a variety of other plants make up the rest of the ground layer.

Unlike the hilly Gowan Farm site, the Brookshead Reserve site (1.3 km south of Brooktondale, NY, elevation: 340 m) is flat to gently sloping, and mesic with occasional wet areas. The most abundant of the goldenrods and asters in the field is *Solidago altissima,* followed in order by *S. rugosa, S. juncea, Aster sagittifolius* Willdenow, *A. lateriflorus, A. novae-angliae* L., *and Euthamia graminifolia.* Other common field species include *Fragaria virginiana* Duchesne, *Potentilla* sp., *Hieracium* sp., *Achillea millefolium* L., *Daucus carota* L., *and Toxicodendron radicans* (L.) Kuntze. In the forest, *S. rugosa* dominates in an area of ca. 30-40 year-old *Acer saccharum* while *S. caesia* is largely restricted to slightly older woods dominated by *Fagus grandifolia, Acer saccharum,* and

Tsuga canadensis (L.) Carriere. Other goldenrods and asters present include *A. divaricatus, A. lateriflorus, S. gigantea,* and *S. bicolor,* the last being largely confined to one dry area. Tree seedlings and woodland herbs such as *Caulophyllum thalictroides, Allium tricoccum* Aiton, and *Podophyllum peltatum* also contribute to the ground flora.

Methods

Goldenrod condition and phenology

To assess aspects of host plant condition and phenology that might affect caterpillar performance, I marked 10 stems of each of the three categories of goldenrod used in this study (*S. rugosa* in fields, *S. rugosa* in forests, and *S. caesia* in forests, henceforth referred to as SRfi, SRfo, and SCfo) and 10 stems of the other abundant field species, *S. altissima,* at Gowan Farm on 15 May 1985. I chose the plants haphazardly from all parts of the study site. Twice per month until late October I measured the plants, noted their condition, and, by referring to threads tied to them as markers, tallied newly emerged leaves and senescing leaves.

Field experiment: Unprotected larvae

To assess the effects of habitat and host plant on caterpillar performance, I conducted larval transfer experiments. Between mid-August and mid-October, 1985, I released *D. leuconotella* caterpillars onto SRfi, SRfo, and SCfo (defined above) and monitored their survival and growth at Gowan Farm and at Brookshead. The caterpillars were progeny of captive moths reared from caterpillars collected in the spring. I hatched and reared the experimental larvae on leaves of *S. altissima.* Given the possibility of larval induction (e.g. Jermy *et al.* 1968), the choice of host species on which to rear larvae for this sort of experiment is problematical. I regarded it best to rear all larvae on the same host species, and on a host species that was clearly suitable for the caterpillar species, in order to assure larvae of matchable size and vigor at the time of setting out. Chemically and nutritionally, *S. altissima* probably resembles *S. rugosa* (SR) more than *S. caesia* (SC) (Hamilton 1989).

I "released" the larvae by taping their leaf refuges onto the plant stems. In this way the larvae had some initial protection from predators and dislodging, which was crucial if they happened to be molting; but as the refuge leaves dried out the caterpillars were forced to wander onto the live plant for food. At Gowan Farm I set out one first or second instar on each of 57 plants of each category (SRfi, SRfo, and SCfo) between 13 and 27 August 1985. I checked each larva after 5 days, 24 days (mid-September), and ca. 44 days (early to mid-October), noting survival, numbers and types of refuges constructed, and numbers of predators on the plants. At Brookshead I set out one second or third instar on each of 61-63 plants of each category between 29 August 1985 and 7 September 1985. I checked these caterpillars after 5 days, 24 days (late September), and ca. 44 days (mid-October). I measured lengths of the caterpillars at both sites before setting out, at the 24 day check, and at the final check, using a dissecting microscope for the first and third measurements but taking the second measurements in the field to minimize disturbance to the larvae.

Field experiment: Caged larvae

To separate the effect of predation from that of food quality in determining survival rates on the three hosts, I gathered growth rate and survival data for *D.*

leuconotella larvae caged in dacron sleeves on SRfi, SRfo, and SCfo at Gowan Farm in August-October 1986. The larvae were again progeny of captive moths reared from caterpillars collected in the spring. For purposes of a more elaborate experiment (see Loeffler 1996b), I used two treatments: one half of the larvae on SRfi, SRfo, and SCfo were removed from their refuges four times, at approximately 10 day intervals, measured, and forced to seek new leaves and rebuild, while the other half of the caterpillars were not disturbed. Manipulation of larvae for measuring did not affect relative growth rates (Loeffler 1996b). The full rationale of the experiment, details of methods used and comparison of the effects of the treatments are given in Loeffler 1996b. The portion of those results which pertains to the present paper, i.e. the relative performance of the repeatedly measured larvae on the different host plant-habitat categories, is given here.

Rates of fall senescence vary among goldenrod species and habitats. In years with early frosts, field plants brown quickly, and the order of senesence among *S. rugosa* and *S. caesia* is first SRfi, then SRfo, and finally SCfo. In years with delayed frost I have noted an order of SRfo, then SRfi, and finally SCfo. To test whether caterpillars would continue feeding and growing larger as long as green leaves were available, and thus derive an advantage from being on SCfo, I maintained the larvae collected after the field experiment for two additional weeks, until late October. Each larva received leaves of the goldenrod species-habitat category and condition (fresh green or dry brown) that it had been feeding on when collected. I kept the larvae in vials in an open, unheated barn, protected from sun but at roughly ambient temperature.

Laboratory observations

To determine whether differences in behavior played roles in the relative success of early instar *D. leuconotella* caterpillars on SRfi, SRfo, and SCfo, I observed their movements, refuge-spinning, and feeding behavior on cut stem tops in the laboratory. The stem tops were placed in water vials to maintain turgidity. In each set of observations I released a caterpillar, matched for size and instar, onto a stem top of each of the three plant categories. Every 15 minutes, for three hours, I noted larval activities (crawling, resting, refuge-making), and I drew transverse cross sections of the caterpillars' refuge leaves to assess relative rates of leaf folding. I used 20 sets of second instars and 20 sets of third or fourth instars. I made additional observations of refuge leaf curvature and feeding at 24 hours. Occasional disappearances of larvae forced removal of the associated matched sets of three larvae from statistical analyses, as indicated by the numbers of degrees of freedom given for the various Friedman Tests in the Results.

The tendency of caterpillars to abandon refuges and seek new ones could compromise survival under natural conditions, because wandering larvae are highly vulnerable to predation and accidental loss of contact with the host (Loeffler, 1996a). To test whether larvae abandoned refuges more often on one goldenrod species-habitat category than another, I maintained them on the cut stem tops for an additional 12 days, watched for predators (none appeared), and counted numbers of refuges spun. Counting refuges in the two field experiments (unprotected and caged) was inadequate to address the effect of host plant and habitat on number of refuge changes because of confounding effects: unprotected caterpillars that abandoned refuges frequently were more likely to be removed by predators during the time interval than were those that stayed in a single refuge, and caged caterpillars sometimes tied leaves to the cage material rather than spinning normal refuges.

Statistics

For statistical analyses I followed methods of Sokal and Rohlf (1981) and Conover (1980), and all computer statistical programs (Statworks™ and Statview 512+™ for MacIntosh) were checked for consistency with sample tests given in these references. ("Mann-Whitney U tests" were not performed in Statworks because they gave discrepant results from Conover (1980) and Statview.) G-statistics were hand-calculated using Williams' correction (Sokal and Rohlf 1981). When followup comparisons were appropriate (i.e., after a significant Friedman test, G-test, or other procedure involving comparison of more than two groups), I either followed methods of the above references or carried out two planned pairwise comparisons, involving SRfi versus SRfo and SRfo versus SCfo. For these two planned but non-independent comparisons, I employed an experimentwise error rate of $\alpha = 1 - (1 - 0.05)^{-2} = 0.0253$ (Sokal and Rohlf 1981).

Results

Goldenrod phenology

Throughout most of the season, comparable amounts of green leaves were available on field and forest goldenrod plants (Fig. 1). Field plants often developed multiple stems and continued producing small new leaves well into August, whereas forest plants halted leaf production in July. However, lower leaves senesced faster on field plants. As a result, the quantity of green leaf tissue available on a given plant was similar between habitats, although leaves were on average smaller and younger on field plants. Insect herbivory was minor on all four goldenrod types. By early fall, deer had nipped off large portions of half of the SCfo plants, thereby either consuming insect herbivores or at least reducing the amount of foliage available to them. SRfi, SRfo, and *S. altissima* (of fields) were less frequently (ca. one in six) and less drastically attacked, such that the effects of deer are not discernable in the data displayed in Fig. 1. Field plants (SRfi and *S. altissima)* browned quickly in early October following a heavy frost; whereas through late October, seven out of 10 SCfo plants and four out of ten SRfo plants remained mostly green and turgid.

Hamilton (1989) gives more extensive data on the phenologies of field and forest goldenrods in the Finger Lakes region of central New York. Although her data do not include SRfo, she found similar growth patterns to those that I observed in SCfo, SRfi, and *S. altissima.* Field plants (SRfi and *S. altissima)* showed more rapid senescence of lower leaves than forest plants including SCfo. SCfo was particularly subject to deer attack. Levels of insect herbivore damage were greater and more variable among populations in field plants.

Field experiment: Unprotected larvae

Surprisingly, early instar *D. leuconotella* survived relatively well on SRfo. At Gowan Farm, survival at 24 days differed significantly among the three host categories ($G_{adj.} = 8.01$, df = 2, $P < 0.025$). Followup comparisons using an experimentwise error rate of $\alpha = 0.025$ indicated significantly higher survival on SRfo than on SCfo ($G_{adj.} = 7.21$, df = 1, $P < 0.025$) and a marginally

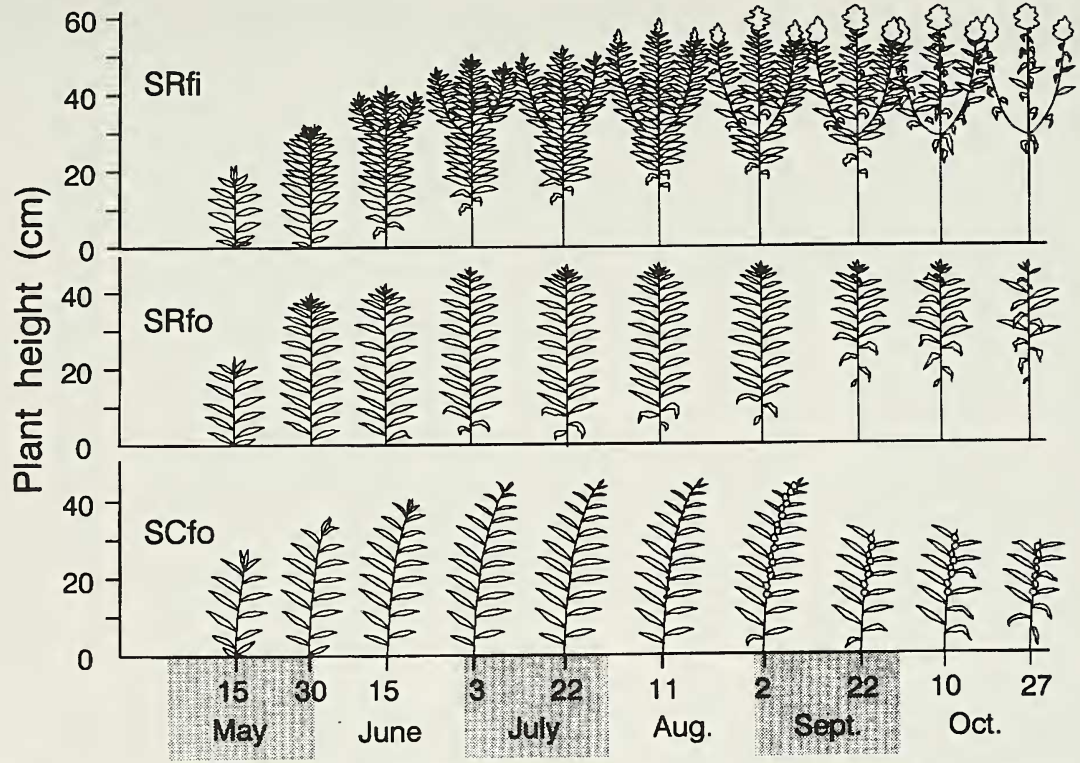

Fig. 1. Phenology of *S. rugosa* in field (SRfi), *S. rugosa* in forest (SRfo), and *S. caesia* in forest (SCfo), averaged from data on heights, branching, numbers of emerging and senescing leaves, and flowering of 10 stems of each type of goldenrod scattered over ca. 40 ha. of varied habitat at Gowan Farm. Data for the other dominant *Dichomeris* host in central New York fields, *S. altissima*, were similar to those for SRfi. The lower average height of SCfo from late September onward reflected extensive deer damage to some of the stems.

nonsignificant difference between SRfo and SRfi (favoring SRfo; $G_{adj.} = 4.07$, df = 1, $0.025 < P < 0.05$). Earlier, larvae on SRfi suffered significantly higher mortality on those than on SRfo between the time of initiating a refuge and the check at 5 days (overall $G_{adj.} = 10.40$, df = 2, $P < 0.01$; for SRfi versus SRfo, $G_{adj.} = 8.94$, df = 1, $P < 0.005$). The slightly larger (second and third instar) larvae released at Brookshead did not show this burst of higher mortality on field plants, and survival was statistically indistinguishable between SRfi and SRfo but lower on SCfo after 24 days (overall $G_{adj.} = 11.68$, df = 2, $P < 0.005$, SRfi versus SRfo: $G_{adj.} = 0.77$, df = 1, $P > 0.1$, SRfo versus SCfo: $G_{adj.} = 11.00$, df = 1, $P < 0.001$) (Fig. 2).

Gowan Farm larvae disappeared from SRfi by early October (Fig. 2), perhaps because the early senescence of field plants at this exposed site following a heavy frost caused larvae to emigrate to ground litter for overwintering. However, SCfo remained green until late October, so the disappearance of larvae from SCfo at both sites could not be attributed to faster plant senescence.

Factors potentially accounting for high mortality on SCfo included high predator loads, unusual larval behavior resulting in greater exposure to predation or other mortality, and poor physiological response to the host plant as a food source. Among these factors, "predation" by other herbivores was indeed relatively severe on SCfo: deer nipped off ten SCfo plants at Brookshead and four SCfo plants at Gowan Farm that had borne caterpillars at the previous check. Heavy feeding by a large tortricid caterpillar apparently dislocated another *Dichomeris* caterpillar from an SCfo plant. No SRfi or SRfo plants were nipped by deer or heavily attacked by other herbivores.

Of true predators the vast majority on all three goldenrod types were spiders, usually small webspinners and salticids. Occasional nabids, reduviids, syrphid larvae, ants, and predaceous mites were also noted. Their numbers did not correlate with low caterpillar survival, however, because they tended if anything to be most abundant on SRfo, on which larval survival was good (Fig. 3).

One aspect of larval behavior, the manner of construction of leaf refuges, differed significantly among goldenrod categories and probably favored larvae on SCfo (Fig. 4). Higher proportions of larvae on the thin-leaved SCfo folded or sharply pinched the leaves, forming roomy refuges ("creases") that the larvae could remain inside to feed. On SRfo leaves, which have thicker veins, and on SRfi leaves, which have much thicker veins and also thicker blades (Loeffler unpublished data), higher proportions of larvae simply spun silk mats ("webs") under which they rested and from which they typically had to emerge to feed. G-tests of relative numbers of creases and folds versus webs on different goldenrod types were significant at both sites (Gowan Farm, $G_{adj.} = 8.198$, df = 2, $P < 0.025$; Brookshead, $G_{adj.} = 9.359$, df = 2, $P < 0.01$). Caterpillars on SRfi were the most likely to bind two leaves to form a "sandwich" refuge, because the leaves on field plants tended to be relatively small and crowded and could be pulled together even by a 2-3 mm

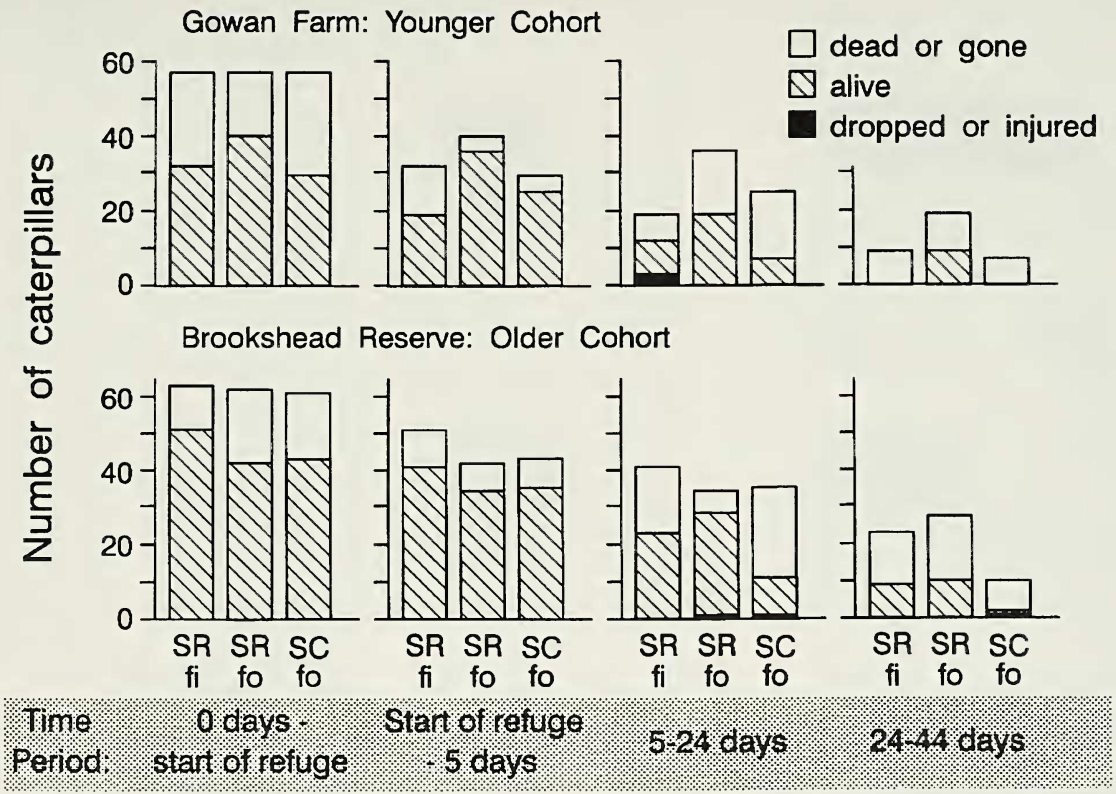

Fig. 2. Survival of unprotected *D. leuconotella* larvae set out as first and second instars in mid-late August at Gowan Farm and as second and third instars at the end of August at Brookshead Reserve. For statistical comparisons see text.

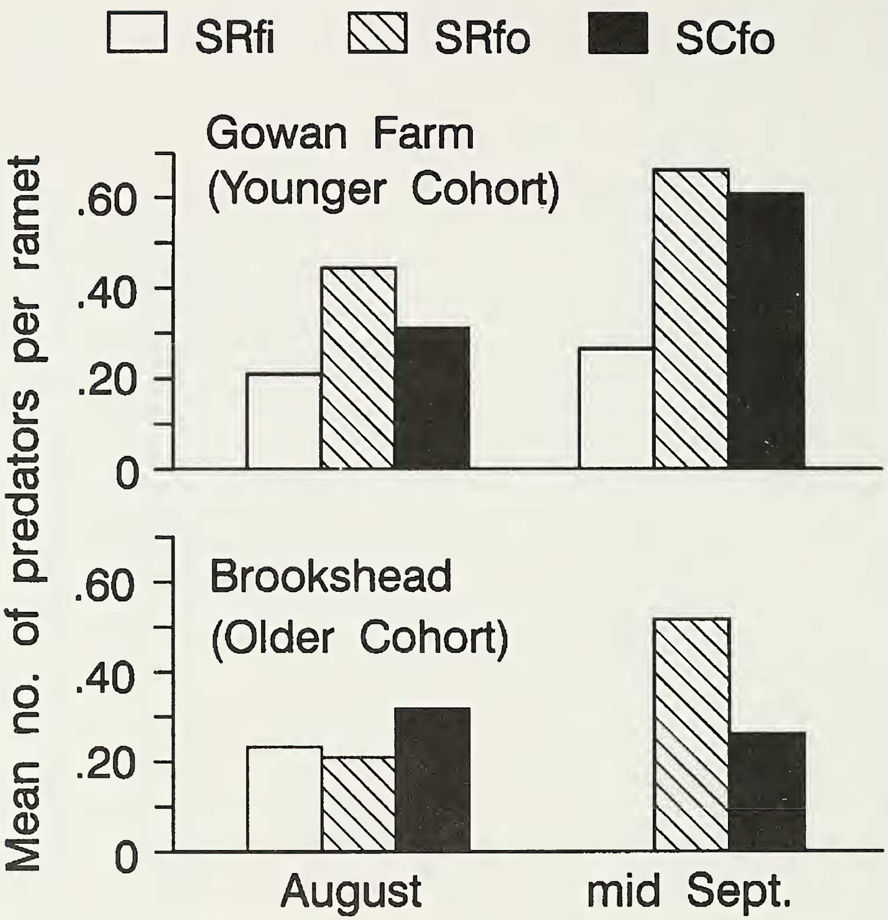

Fig. 3. Mean numbers of predators per goldenrod ramet during three sampling periods at the two experimental sites in late summer, 1985. G-tests comparing predator abundance among goldenrod host-habitat categories gave nonsignificant results for August but significant or nearly significant results in September (Gowan Farm: overall $G_{adj.} = 8.756$, df = 2, $P < 0.025$; followup comparison of SRfi versus SRfo, $G_{adj.} = 7.247$, df = 1, $P < 0.01$; SRfo versus SCfo, no significant difference. Brookshead: overall $G_{adj.} = 5.469$, df = 2, $P < 0.1$.).

caterpillar. Such "sandwiches" enclosed an amount of enclosed leaf tissue intermediate to that within a web and that within a crease or fold.

There were no differences among hosts or habitats in number of refuges constructed (usually 1-3 refuges per larva over the first ca. 24 days) and amount of feeding. Differential survival may however have obscured differences in these behaviors (see Laboratory Observations below).

First and early second instars grew poorly on SCfo. Among the younger

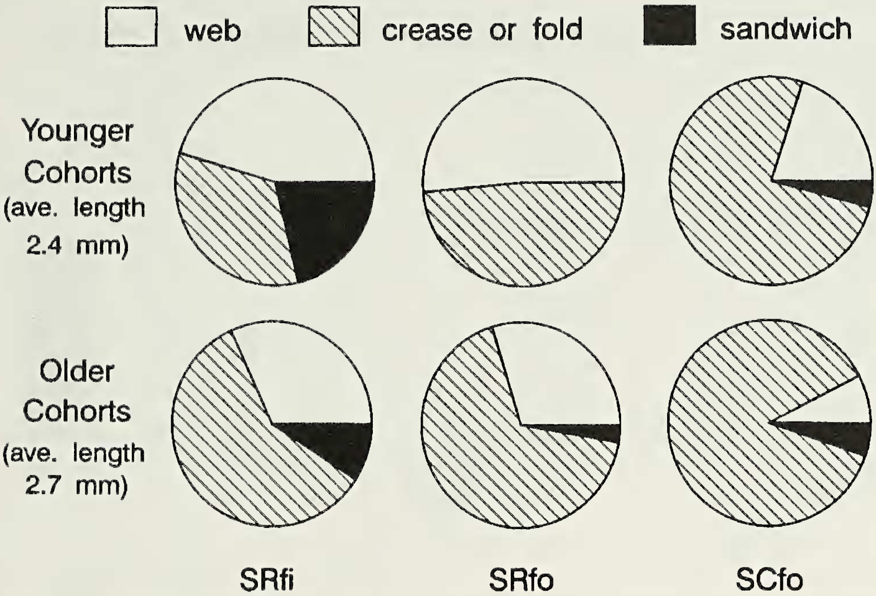

Fig. 4. Relative numbers of *D. leuconotella* caterpillars constructing each of three refuge types over the first five days after release on field and forest goldenrods in late summer, 1985. Younger cohorts were first and second instar larvae released at Gowan Farm; older cohorts were second and third instar larvae released at Brookshead Reserve. For each pie graph, n = 38 to 52 depending on number of larvae surviving five days on that goldenrod host-habitat category (Fig. 2).

cohort set out at Gowan Farm, survivors to mid September grew significantly less on SCfo than on SRfi or SRfo (ANOVA: $F_{(\text{host category})} = 4.344$, df = 2,32, $P = 0.021$); indeed, many larvae shrank (Fig. 5). No first instars survived 24 days, and survival through 24 days of the mixed group of first and second instars was significantly associated with larger initial size (Kruskal-Wallis test: $T = 7.030$, $P = 0.008$). On SRfi or SRfo, in contrast, many first instars survived; the associations of survival with greater initial size were weak and nonsignificant (Kruskal-Wallis tests, SRfi: $P = 0.125$, SRfo: $P = 0.075$). The slightly older (second to third instar) larvae at Brookshead grew as well on a diet of SCfo as on SRfi and SRfo (Fig. 5) (ANOVA: $F_{(\text{host category})} = 1.552$, df = 2,57, $P = 0.221$). Survival to late September in this older group was not significantly related to initial size on any of the three host-habitat categories (Kruskal-Wallis tests: $P >> 0.05$).

Field experiment: Caged larvae

Data on larvae protected from predators confirmed that very young larvae had high host-related mortality on SCfo. Disappearance rates of larvae released as second instars were significantly higher on this host (Fig. 6; at mid Sept. check before significant host senescence, $G_{adj.} = 22.97$, df = 2, $P << 0.001$; SRfo versus SCfo, $G_{adj.} = 11.30$, df = 1, $P < 0.001$; SRfi versus SRfo, $P > 0.1$).

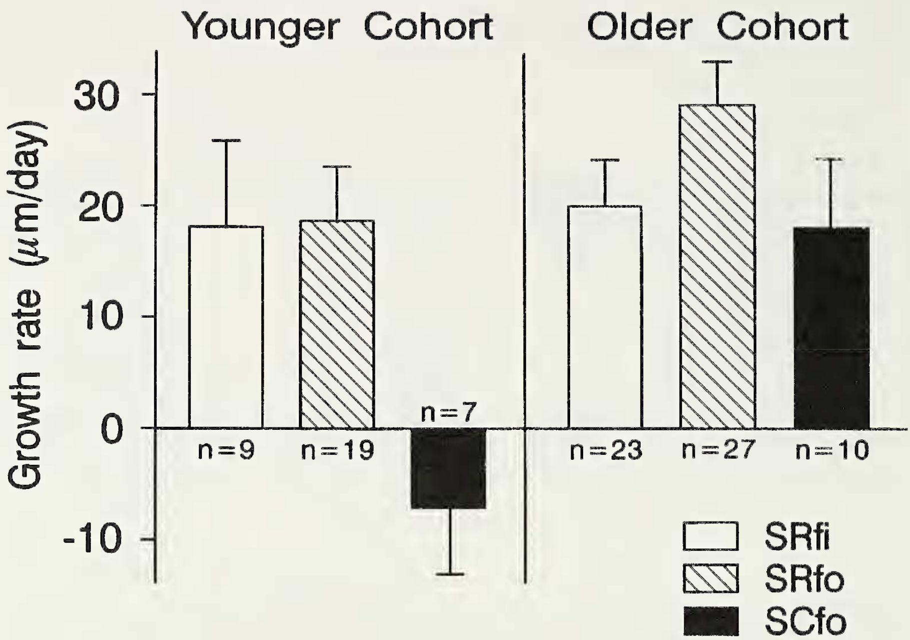

Fig. 5. Rates of growth in length (means and standard errors) of unprotected *D. leuconotella* caterpillars surviving a ca. 24 day period on field and forest goldenrods in late summer, 1985. (For calculation of daily growth rate, growth in length was assumed to be linear with time. Laboratory measurements suggest that this assumption is approximately correct for small larvae in late summer.)

Usually, caterpillars that disappeared had been either shrinking or at least failing to grow. I searched the cages with great care at each check and was sometimes able to locate 1-2 mm, shriveled and blackened corpses. Among the older (third and fourth instar) larvae of the second group survival was however comparable to that on SRfi and SRfo (Fig. 6).

Growth rates of surviving larvae (Fig. 6) corroborated the results for unprotected larvae. Larvae released as second instars grew at similar rates on SRfi and SRfo but immediately showed lower growth rates on SCfo, and their cumulative growth rates remained significantly lower on SCfo for a month (ANOVAs: $P < 0.05$ for time of release to first, second, and third checks, $P > 0.05$ for time of release to fourth and fifth checks). By October all of the larvae which grew poorly on SCfo had died, leaving just one larva that had grown through the season at rates comparable to the average rates on SRfi and SRfo. Growth rates of third and fourth instars (older cohort), however, were similar for most of the season on the three host plant categories (ANOVAs, $P > 0.05$).

Although SCfo remained green longer into October than did SRfi or SRfo, its delayed senescence provided no advantage to the caterpillars. During

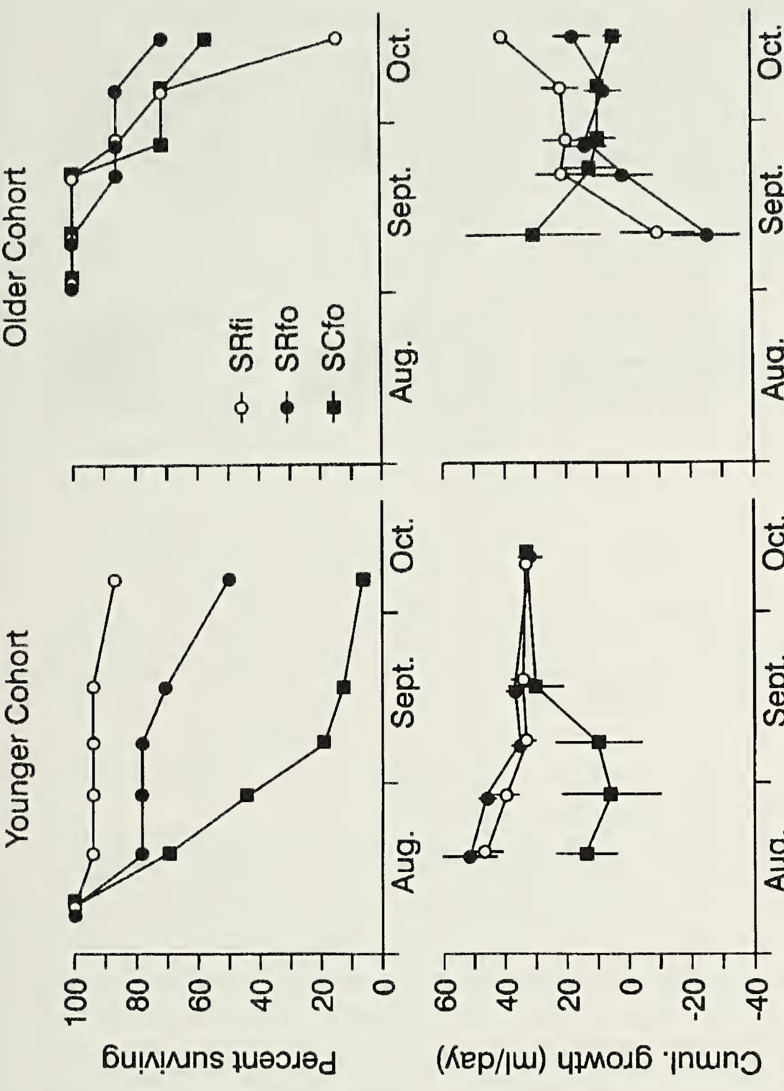

Fig. 6. Survival and rates of growth in length (means ± S.E.) of *D. leuconotella* caterpillars released as second instars ("Younger Cohort") and third and fourth instars ("Older Cohorts") on caged field and forest goldenrods at Gowan Farm in late summer, 1986. Initial cohort sizes were 15 younger larvae or 8 older larvae on each category of host plant and habitat.

October the caterpillars simply shortened and thickened in preparation for winter, at even rates regardless of goldenrod type or degree of senescence (Kruskal Wallis test: T = 0.640, P = 0.959).

Laboratory observations

Second instars placed onto cut stem tops and monitored for three hours behaved differently depending on host type. Larvae on SCfo spent relatively more time crawling over the stem top; larvae on SRfo spent relatively more time resting; and larvae on SRfi spent relatively more time applying silk to

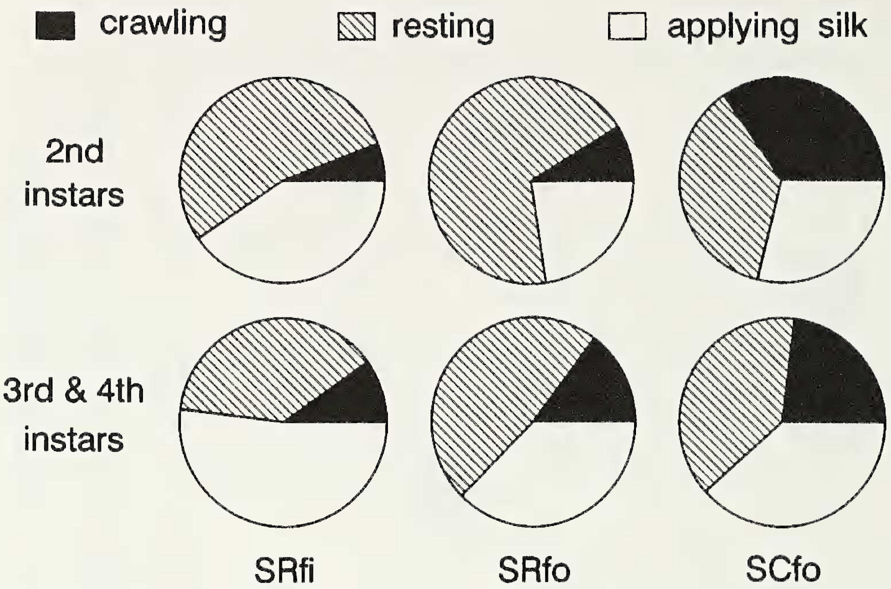

Fig. 7. Average proportions of time spent in each of three activities by young *D. leuconotella* larvae released onto cut stem tops of SRfi, SRfo, and SCfo and monitored at 15-minute intervals for three hours. Statistical comparisons are given in Table 1.

construct refuges (Fig. 7, Table 1). Third and fourth instars showed similar but less pronounced trends (Fig. 7, Table 1).

Despite their extensive wandering before starting refuges, early instars on SCfo fed as promptly as those on SRfi and SRfo (second instars, Friedman test: $T_2 = 2.102$, df = 2,34, $P > 0.10$; third and fourth instars, Friedman test: $T_2 = 2.825$, df = 2,24, $P > 0.10$). In fact, if a trend existed, it was for larvae to be slowest to feed on SRfi in both age groups. As in field experiments, larvae appeared to consume similar amounts of foliage of the three goldenrod categories during subsequent days.

Differences in leaf morphology appeared to account for the slowness of larvae to settle down on SCfo. Larvae consistently began refuges in cracks or crevices when they were available. On *S. rugosa* (SRfi and SRfo), every leaf had such a crevice where the midrib and the underside of the blade met at a sharp angle, and many leaves had smaller crevices along side veins. Virtually all refuges were constructed in those spots. However, *S. caesia* (SCfo) midribs tapered smoothly and met the blade at a shallow angle in cross section; and the small side veins created no crevice at all. Three larvae on SCfo began spinning relatively quickly (within 45 minutes) when they encountered cracks between axillary flowerbuds and leaves. But these refuge sites were too small for long-term habitation, and two of the three larvae abandoned these refuges within a day.

Table 1. Results of Friedman tests and and followup multiple comparisons (Conover 1980) comparing activity of early instar *D. leuconotella* caterpillars on cut stem tops of SRfi, SRfo, and SCfo (n = 19 second instars or 15 third and fourth instars on each host plant-habitat category).

Comparison		T_2	df	P
Second instars				
Proportion of time spent crawling, SRfi, SRfo, SCfo		10.577	2, 36	$P < 0.01$
followup comparisons:	SRfi = SRfo			ns
	SCfo > SRfi			$P < 0.001$
	SCfo > SRfo			$P < 0.001$
Proportion of time spent resting, SRfi, SRfo, SCfo		6.333	2, 36	$P < 0.01$
followup comparisons:	SRfo > SRfi			$P < 0.05$
	SRfi = SCfo			ns
	SRfo > SCfo			$P < 0.002$
Proportion of time spent spinning, SRfi, SRfo, SCfo		5.252	2, 36	$P < 0.025$
followup comparisons:	SRfi > SRfo			$P < 0.005$
	SRfi > SCfo			$P < 0.02$
	SRfo = SCfo			ns
Third and fourth instars				
Proportion of time spent crawling, SRfi, SRfo, SCfo		3.343	2, 28	$P < 0.01$
followup comparisons:	SRfi = SRfo			ns
	SCfo > SRfi			$P < 0.05$
	SCfo = SRfo			ns
Proportion of time spent resting, SRfi, SRfo, SCfo		0.924	2, 28	ns
Proportion of time spent spinning, SRfi, SRfo, SCfo		2.846	2, 28	ns

A positive aspect of SCfo as a host was that its leaves could be folded much more rapidly into a protective chamber than could the thicker-veined leaves of SRfo or the substantially thicker leaves of SRfi. Hence, although second-instar larvae typically began applying silk half an hour or more later on SCfo than on SRfi or SRfo (median times for starting refuges 1.25 hours on SCfo and 0.5 hours on SRfi or SRfo), the leaves were on average more curved on SCfo at three hours and considerably more curved at 24 hours (Table 2). By 24 hours many second-instar larvae on SCfo had folded the leaf to a right angle or more, whereas those on SRfi or SRfo had barely bent the leaf. Third or fourth instars also folded SCfo leaves fastest; in addition, with their greater abilities they folded SRfo leaves detectably more sharply than SRfi leaves in 24 hours (Table 2).

Over the next 12 days, second-instar larvae abandoned their refuges for new ones significantly more often on SCfo and SRfi than on SRfo (Fig. 8). The readiness to abandon refuges on SRfi may have been due to a higher rate of drying and browning of SRfi stem tops (91% of refuges showed browning around feeding scars and 48.5% of stem tops showed partial to substantial

Table 2. Results of Friedman tests comparing relative change in leaf curvature achieved by early-instar *D. leuconotella* caterpillars folding leaves on cut stem tops of SRfi, SRfo, and SCfo (n = 18 second instars or 14 third and fourth instars on each host plant-habitat category).

Comparison		T_2	df	P
Second instars				
Change in leaf curvature at 3 hrs, SRfi, SRfo, SCfo		28.737	2, 34	$P \ll 0.01$
followup comparisons:	SRfi = SRfo			ns
	SCfo > SRfi			$P < 0.001$
	SCfo > SRfo			$P < 0.001$
Change in leaf curvature at 24 hrs, SRfi, SRfo, SCfo		70.665	2, 34	$P \ll 0.01$
followup comparisons:	SRfi = SRfo			ns
	SCfo > SRfi			$P < 0.001$
	SCfo > SRfo			$P < 0.001$
Third and fourth instars				
Change in leaf curvature at 3 hrs, SRfi, SRfo, SCfo		8.000	2, 26	$P < 0.01$
followup comparisons:	SRfi = SRfo			ns
	SCfo > SRfi			$P < 0.001$
	SCfo > SRfo			$P < 0.02$
Change in leaf curvature at 24 hrs, SRfi, SRfo, SCfo		10.908	2, 26	$P < 0.01$
followup comparisons:	SRfo > SRfi			$P < 0.05$
	SCfo > SRfi			$P < 0.001$
	SCfo > SRfo			$P < 0.05$

senescence, compared to 71% and 11% respectively on SRfo stem tops). But SCfo stem tops senesced least rapidly of the three types (32% of refuges showed some browning; all stem tops however remained green and turgid). Hence some other characteristic of SCfo apparently triggered larvae to abandon their refuges. As in previous results, third and fourth instars were less affected than second instars by differences among the three host categories (Fig. 8).

Discussion

Two factors—food quality and leaf morphology—appeared to strongly affect the performance of early instar *D. leuconotella* larvae on forest and field goldenrods. Both of these factors varied more significantly between host plant species than between habitats. Indeed, on the same host plant species (SR or *S. rugosa)*, caterpillars tended to fare slightly better in forest than in their usual field habitat.

Early instar *D. leuconotella* caterpillars had generally comparable growth rates on SRfi and SRfo, a perhaps surprising result given documented differences in food quality between sun and shade leaves of various other plant species (Lincoln and Langenheim 1979, Louda and Rodman 1983,

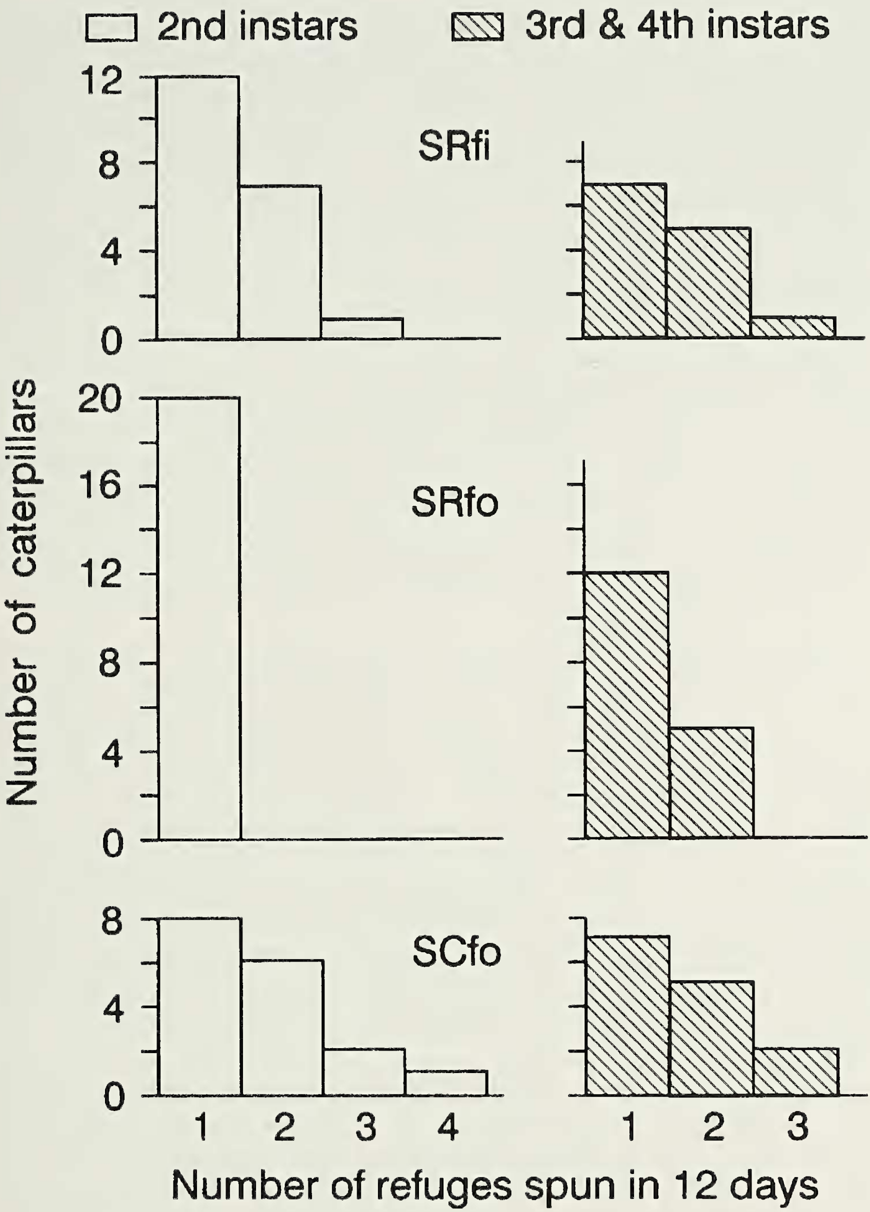

Fig. 8. Numbers of refuges built by early instar *D. leuconotella* larvae over 12 days (late summer-fall, 1987) on cut stem tops of SRfi, SRfo, and SCfo. G-tests were highly significant for second instars, both overall and in followup comparisons of SRfo versus SRfi and SRfo versus SCfo ($P < 0.005$); but a G-test for third and fourth instars was not significant ($P > 0.05$).

Schultz 1983 and references therein, Bultman and Faeth 1988, Dudt and Shure 1994). On *S. caesia* (SCfo), however, first and second instars suffered poor growth rates and high mortality. SCfo differs chemically and nutritionally from SRfi: water and nitrogen contents are higher, but so are tannins and fiber on a percent dry matter basis (Hamilton, 1989). Other aspects of SCfo's secondary chemistry (e.g., presence of alkaloids) are little known (Hamilton, 1989). A common chrysomelid beetle, *Trirhabda virgata,* that feeds in June and July on field goldenrod species, also survives and grows poorly on SCfo (Messina 1983, Hamilton 1989). Among the several species of insect herbivores that do develop successfully on SCfo is one other *Dichomeris* species, *D. bilobella,* (Hamilton 1989, Loeffler 1994), which grows at comparable rates on SCfo, SRfo, and SRfi (Loeffler 1992). *Dichomeris leuconotella* also seems able to thrive on SCfo from the third instar onward, although caterpillars raised through their later instars on SCfo tended to develop into smaller and later-eclosing adults (Loeffler 1992 and unpublished data). All instars of *D. leuconotella* feed readily on SCfo. Thus, the chemical aspect of SCfo that negatively affects the youngest larvae is not a component that can be avoided by small mouthparts (e.g., Reavey 1993 and references therein); nor is it a strong feeding deterrent.

Leaf morphology strongly affected larval behavior, which in turn affected larval vulnerability to predation and to accidental dislocation from the host plant. Staged encounters using some of *D. leuconotella's* most common predators suggested that early instars, though most secure when in their refuges, also tend to escape predator notice when resting quietly without a refuge (Loeffler 1996a). In the present study, therefore, larvae on SRfo behaved in ways that should minimize predation, resting quietly much of the time, wandering less than on SCfo, and spending less time actively applying silk than on SRfi. The thinness of forest leaves was advantageous; larvae could complete refuges faster on forest plants than on field plants despite spending less time per hour in spinning. This difference may account for relatively high mortality of first and second instars on SRfi during construction of their first refuges.

On SCfo, caterpillars could fold leaves even more rapidly than on SRfo, but this advantage appeared to be counteracted by their prolonged wandering to find refuge sites and their tendency to abandon refuges frequently and seek new ones. Prolonged wandering of caterpillars on SCfo appeared to be a response to the shallow, poorly-defined crevices beside leaf veins that are characterisitic of this goldenrod species. Those few caterpillars that encountered a relatively sheltered spot on SCfo (between an axial flowerhead and a leaf base) settled down to spin there quickly—although such spots were too small to be used for long. This tendency to seek out the most sheltered site available in which to spin a refuge is typical for early instar *D. leuconotella;* I have found them inhabiting leafy cecidomyiid galls, leaf mines of *Cremastobombycia solidaginis* (Lepidoptera: Gracillariidae), and leaf ties of a variety of other caterpillars including the previous generation of *Dichomeris*

(Loeffler 1994). Damman (1987) and Cappuccino (1993) also reported tendencies of early instar leaf-tying caterpillars to inhabit premade shelters, or of adult moths to oviposit in old leaf ties; and Cappuccino (1993) verified that first instars of the birch tube-maker *Acrobasis betulella* Hulst. (Lepidoptera: Pyralidae) had higher survival rates when inhabiting such spaces. In the absence of such shelters, *D. leuconotella* larvae invariably build their refuges in the crevice alongside a vein; but such crevices must apparently be of a certain depth to be attractive as refuge sites, and those on *S. caesia* (SCfo) are shallower than those of *S. rugosa* (both SRfi and SRfo, unpublished data) or of the other common, field-inhabiting goldenrods that are normally used as hosts.

Some other elements of leaf morphology, in particular trichomes, have been shown to have striking effects on caterpillar behavior and survival (Levin 1973, Southwood 1986 and references therein, Woodman and Fernandes 1991). In the present study, trichomes had no obvious positive or negative effects; caterpillars readily held onto and negotiated both the hairy leaves of *S. rugosa* (SRfi and SRfo) and the smooth leaves of *S. caesia* (SCfo) (pers. observ.). It is conceivable that the presence of trichomes on *S. rugosa* enhanced the caterpillars' tactile sensation of being in crevices and increased their willingness to settle down and spin refuges.

In their need for sheltered spots or deep crevices, *D. leuconotella* caterpillars may be mismatched phenologically with SCfo. Only two species of leaf-folding caterpillars specializing on *Solidago* and *Aster* use *S. caesia* (SCfo) as a host: *D. bilobella* (Zeller) and the oecophorid *Agonopterix pulvipennella* (Clemens) (Hamilton 1989, and pers. observ.). Early instars of both species are found only in spring, when they can (and do) find crevices for starting refuges in the leafy terminal buds (Loeffler 1994). Other goldenrod-feeding *Dichomeris* species in central New York hatch in summer and overwinter as partly grown larvae (Hodges 1986, Loeffler 1994); and none of them is known to use SCfo as a host—not even *D. ochripalpella* (Zeller), which unlike *D. leuconotella* often develops on forest plants (Loeffler 1994).

The poor survival and growth of early instar *D. leuconotella* on SCfo thus appears related to host plant attributes rather than to effects of habitat. Older instars show similar survival patterns on SRfi, SRfo, and SCfo, although for slightly different reasons (Loeffler 1992 and unpublished data), and I will argue in presentation of those data that the most likely explanation for *D. leuconotella's* absence from forest habitat is not that immature stages cannot survive there, but that suitable hosts (i.e., goldenrods and asters other than *S. caesia* (SCfo), on which adults are reluctant to oviposit; Loeffler 1994) are more concentrated in open areas. In one of the few other studies addressing the relationship of performance of uncaged larvae and larval habitat restriction, Rausher (1979) reached a similar conclusion with regard to certain papilionid butterflies: adults of two species laid eggs only in sunny habitats, where host plants were more

abundant, although their larvae had better survival rates when transferred to host plants in forest.

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